Growth and yield of all-aged Douglas-fir – western hemlock forest stands: a matrix model with stand diversity effects

Jingjing Liang, Joseph Buongiorno, and Robert A. Monserud

Abstract: A density-dependent matrix model was developed for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) – western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forest stands in the Pacific Northwest of the United States. The model predicted the number and volume of trees for 4 species groups and 19 diameter classes. The parameters were based on species-dependent equations linking individual tree growth, mortality, and stand recruitment to tree and stand characteristics, including stand diversity in terms of tree species and size. The equations were estimated with individual tree and stand data from 2706 permanent plots in western Washington and Oregon, largely from private and state lands, measured twice at an average interval of 10 years. Other things being equal, diameter growth increased slightly with species diversity and decreased with size diversity. Recruitment increased with species diversity and decreased with size diversity. Mortality was independent of species diversity and tended to increase with size diversity. There was practically no relationship between individual tree volume and species or size diversity. The number of trees predicted by the model over the interval between successive inventories was generally unbiased. Long-term predictions with different initial conditions were consistent with standard yield tables and compared favorably with those of the Forest Vegetation Simulator. The model also implied that, independently of its initial condition, an undisturbed stand would eventually reach a steady state dominated by western hemlock more than 1 m in diameter, with few trees of other species and size.

Résumé : Un modèle matriciel dépendant de la densité a été développé pour des peuplements de douglas (*Pseudotsuga menziesii* (Mirb.) Franco) et de pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) dans la région du Nord-Ouest du Pacifique aux États-Unis. Le modèle prédit le nombre d'arbres et leur volume pour quatre groupes d'espèces et dix-neuf classes de diamètre. Les paramètres sont basés sur des équations dépendantes des espèces reliant la croissance individuelle des tiges, la mortalité et le recrutement à l'intérieur des peuplements aux caractéristiques des arbres et des peuplements, incluant la diversité des peuplements en termes d'espèce et de taille des arbres. Les équations ont été estimées à partir de données d'arbres individuels et de peuplements provenant de 2706 parcelles échantillons permanentes localisées dans l'ouest des États de Washington et de l'Oregon, principalement sur des terrains privés ou appartenant à l'État, et qui ont été mesurées deux fois à intervalle moyen de 10 ans. Toutes choses étant égales, la croissance en diamètre a augmenté légèrement avec la diversité spécifique et elle a diminué avec la diversité en taille. Le recrutement a augmenté avec la diversité spécifique et il a diminué avec la diversité en taille. La mortalité était indépendante de la diversité spécifique et tendait à augmenter avec la diversité en taille. Il n'y avait pratiquement pas de relation entre le volume individuel des arbres et la diversité spécifique ou en taille. Le nombre d'arbres prédit par le modèle dans l'intervalle entre des inventaires successifs était généralement non biaisé. Les prédictions à long terme avec différentes conditions initiales étaient consistantes avec les tables de rendement standard et se comparaient favorablement à celles du modèle « Forest Vegetation Simulator ». Le modèle assumait aussi qu'un peuplement non perturbé, indépendamment de sa condition initiale, atteindrait éventuellement un état stable dominé par des pruches de l'Ouest de plus de un mètre de diamètre, avec peu d'arbres d'autres espèces ou dimensions.

[Traduit par la Rédaction]

Introduction

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) – western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) is one of the most productive forest types in North America (Curtis and Carey 1996). These forests occupy a wide range of environments, from the wet coastal Cascade Mountains to the dry interior mountains and plateau (Franklin and Dyrness 1988), and vary highly in composition and structure (Barbour and Billings 1988). They are mostly forests in seral stages but there are still some areas of old growth with massive Douglas-fir and western hemlock trees. Although other species are present,

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Table 1. Frequency of tree species in all sample plots.

Common name	Scientific name[a]	Frequency (%)
Douglas-fir	*Pseudotsuga menziesii*	41.27
Other shade-intolerant species	—	24.07
Red alder	*Alnus rubra*	10.85
Ponderosa pine	*Pinus ponderosa*	7.10
Lodgepole pine	*Pinus contorta*	1.94
Western larch	*Larix occidentalis*	0.92
Black cottonwood	*Populus balsamifera* subsp. *trichocarpa*	0.72
Pacific madrone	*Arbutus menziesii*	0.63
Incense-cedar	*Calocedrus decurrens*	0.44
Oregon white oak	*Quercus garryana*	0.42
Western juniper	*Juniperus occidentalis*	0.26
Oregon ash	*Fraxinus latifolia*	0.25
Noble fir	*Abies procera*	0.18
Quaking aspen	*Populus tremuloides*	0.15
Western white pine	*Pinus monticola*	0.14
Sugar pine	*Pinus lambertiana*	0.05
Jeffrey pine	*Pinus jeffreyi*	0.01
Western hemlock	*Tsuga heterophylla*	18.80
Other shade-tolerant species	—	15.86
Western redcedar	*Thuja plicata*	5.88
Bigleaf maple	*Acer macrophyllum*	3.09
Grand fir	*Abies grandis*	2.09
Sitka spruce	*Picea sitchensis*	1.44
Pacific silver fir	*Abies amabilis*	1.32
White fir	*Abies concolor*	0.94
Mountain hemlock	*Tsuga mertensiana*	0.42
Engelmann spruce	*Picea engelmannii*	0.34
Subalpine fir	*Abies lasiocarpa*	0.17
Port Orford cedar	*Chamaecyparis lawsoniana*	0.12
Pacific yew	*Taxus brevifolia*	0.03
Alaska yellowcedar	*Chamaecyparis nootkatensis*	0.02
Redwood	*Sequoia sempervirens*	0.01
All species	—	100.00

[a]Nomenclature per Little (1979).

such as red alder (*Alnus rubra* Bong.), western redcedar (*Thuja plicata* Donn ex D. Don), bigleaf maple (*Acer macrophyllum* Pursh), and grand fir (*Abies grandis* Dougl. ex D. Don) (Table 1), Douglas-fir makes up 66% of the total volume of all species, which is estimated at 1.2×10^9 m^3 (McArdle et al. 1961). Western hemlock is another important commercial species. It is shade tolerant yet fast growing, deer and elk browse it, and hemlock trees are a part of the esthetics of western forests (Burns and Honkala 1990).

Even-aged silviculture is prevalent in managed Douglas-fir forests. There has been little tendency to adopt uneven-aged (selection) management (Emmingham 1998), despite its attractive features (Hansen et al. 1991; Guldin 1996). This seems to be due to a lack of experience with uneven-aged management and scarcity of data regarding its effects compared with even-aged systems. The objective of the present study was to develop a model to help predict the development of Douglas-fir – western hemlock stands with various types of silviculture.

Among existing models, the Forest Vegetation Simulator (FVS; Wykoff et al. 1982; Teck et al. 1997) has a long history as a stand management tool. Six geographic variants of FVS are available for the Pacific Northwest (Ritchie 1999). Although the North Idaho variant has been used to optimize the management of uneven-aged mixed-conifer stands with natural regeneration (Haight and Monserud 1990), the lack of a regeneration module in the other variants precludes long-term applications. The Douglas-fir Simulator (DFSIM), a simulator for managed stands dominated by Douglas-fir (Curtis et al. 1981, 1982) has the same shortcoming and possible problems in predicting mortality (Ritchie 1999). The age dependence of SPS, an individual-tree simulator originally developed for Douglas-fir in Oregon and Washington (Arney 1985), hinders its application to uneven-aged stands, where tree age is often unknown. FPS is an individual-tree spatial model that predicts stand growth up to 100 years only (Arney 1995), and thus it is not suitable for steady-state analysis. A forest gap model based on ZELIG (Urban et al. 1991) is also available for western Oregon (Busing and Garman 2002; Garman et al. 2003; Garman 2004). Gap models simulate species-level dynamics on small forest plots (0.04 ha) over long time periods and are primarily used to examine long-term forest succession and test ecological theory (Monserud 2003*a*). Additional stand and landscape forest models in the

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Fig. 1. Geographic distribution of the Forest Inventory and Analysis (FIA) plots used to calibrate the growth and yield model for all-aged Douglas-fir – western hemlock stands. (Location is based on the plot coordinates from the Pacific Northwest - FIA Integrated Database (version 1.4). Courtesy of Mo Zhou.)

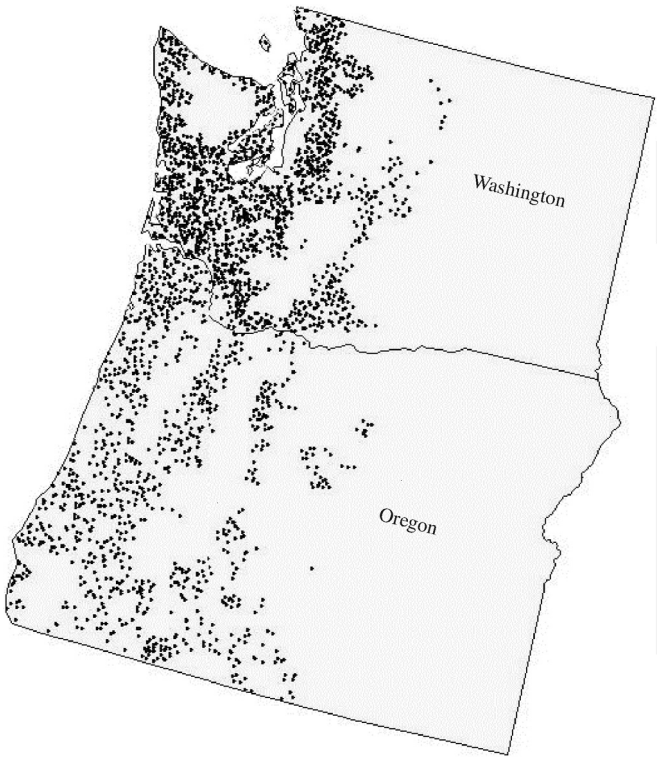

Table 2. Distribution of plots by ownership.

Ownership	No. of plots	Proportion (%)
Private	2136	78.9
Public		
State	438	16.2
Local government	67	2.5
Other federal owner	29	1.1
Bureau of Land Management	20	0.7
National Park Service	16	0.6
Total	2706	100.0

region are reviewed by Monserud (2003*b*, 2003*c*) and Robinson and Monserud (2003).

The purpose of this paper is to describe a model for predicting the growth and yield of all-aged Douglas-fir – western hemlock stands west of the Cascade Mountains in Oregon and Washington. In the process, we report on the effects of tree and stand characteristics, including stand diversity, on tree diameter growth, recruitment, and mortality.

This diameter-class, species-specific, nonspatial model is similar to earlier models of forest stands (e.g., Adams and Ek 1974; Buongiorno and Michie 1980). It is a direct extension of Ralston et al. (2003), with four instead of two species groups, an improved model of recruitment to recognize the many instances where there is no recruitment, the inclusion of both even-aged and uneven-aged stands, and a much more extensive database. To deal better with a wide variety

Table 3. Summary statistics for plot data.

	Douglas-fir (trees·ha^{-1})	Other shade-intolerant spp. (trees·ha^{-1})	Western hemlock (trees·ha^{-1})	Other shade-tolerant spp. (trees·ha^{-1})	Site productivity (m^3·ha^{-1}·year^{-1})	Inter-inventory period (years)	Basal area (m^2·ha^{-1})	Recruitment (trees·ha^{-1}·year^{-1})				Species diversity (H_s)	Size diversity (H_d)	Total volume (m^3·ha^{-1})
								Douglas-fir	Other shade-intolerant spp.	Western hemlock	Other shade-tolerant spp.			
Mean	213.28	154.12	140.22	101.82	10.32	10.53	27.32	5.49	3.82	3.30	2.50	0.54	1.65	331.21
SD	300.59	261.11	295.39	216.26	5.05	0.90	17.04	18.07	15.69	14.01	11.06	0.39	0.63	251.06
Max.	3077.66	4896.28	3020.64	2607.80	21.00	23.00	96.11	256.47	408.02	238.92	237.94	1.38	2.76	1547.95
Min.	0.00	0.00	0.00	0.00	0.70	9.00	0.55	0.00	0.00	0.00	0.00	0.00	0.00	1.97
n	2706	2706	2706	2706	2706	2706	2706	2706	2706	2706	2706	2706	2706	2706

Note: Level variables are at the time of the first inventory, recruitment is between the two inventories.

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Table 4. Summary statistics for individual tree data.

	Douglas-fir	Other shade-intolerant spp.	Western hemlock	Other shade-tolerant spp.
Diameter (cm)				
Mean	38.82	30.50	32.95	40.80
SD	21.32	16.07	19.54	27.15
Max.	207.80	130.60	173.65	304.55
Min.	3.98	3.98	3.98	3.98
n	23161	11831	11612	8900
Diameter growth (cm·year^{-1})				
Mean	0.70	0.45	0.59	0.58
SD	0.43	0.36	0.39	0.44
Max.	13.97	16.43	9.58	8.47
Min.	–0.01	–0.29	0.00	–1.15
n	23161	11831	11612	8900
Mortality rate (year^{-1})				
Mean	0.003	0.006	0.003	0.004
SD	0.016	0.023	0.017	0.019
Max.	0.111	0.111	0.111	0.111
Min.	0.000	0.000	0.000	0.000
n	23838	12650	12007	9295
Volume (m^3·tree^{-1})				
Mean	2.20	1.12	1.73	2.36
SD	2.82	1.47	2.56	4.37
Max.	56.26	22.39	38.32	165.00
Min.	0.01	0.01	0.01	0.00
n	23161	11831	11612	8900

Note: Diameter and volume are at the time of the first inventory, diameter growth and mortality rate are between the two inventories.

of stand structures we account explicitly for the potential effects of stand diversity (in terms of tree species and size) on the growth, mortality, and recruitment of trees in forest stands. Although the hypothesis of a positive effect of diversity on ecosystem productivity and stability has been tested in grasslands in particular (Tilman and Downing 1994; Tilman et al. 1996, 1997; Cardinale et al. 2004), this seems to have been scarcely done in forest ecosystems (Piazza 1999).

Methods

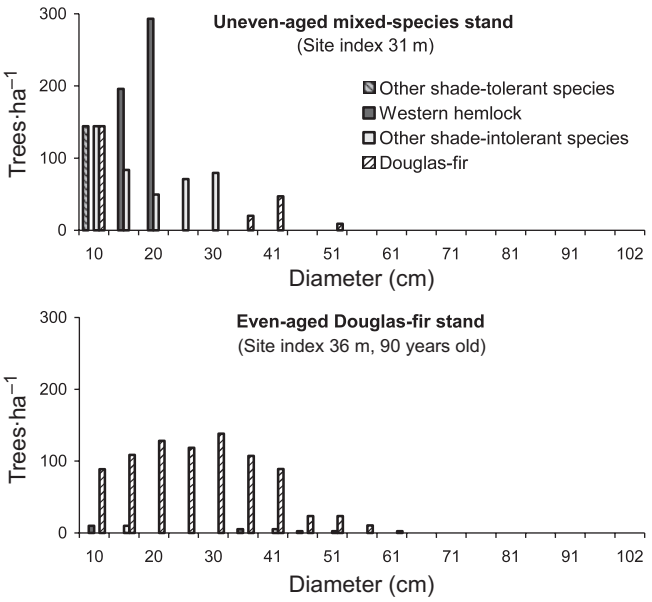
Model structure

The growth model has the following form:

$$[1] \qquad \boldsymbol{y}_{t+1} = \mathbf{G}\boldsymbol{y}_t + \boldsymbol{r} + \boldsymbol{\epsilon}_t$$

where $\boldsymbol{y}_t = [y_{ijt}]$ is a column vector representing the number of live trees in species group i (i = 1, 2, 3, 4) and diameter class j (j = 1, 2,…,19) at time t, per unit of land area. $\mathbf{G}$ is a state-dependent matrix that describes how the trees grow or die between t and t+1. $\boldsymbol{r}$ is a state-dependent vector representing the number of trees recruited in the smallest diameter class of each species group, between t and t+1 and $\boldsymbol{\epsilon}_t$ is a vector of random shocks. As a result of the dependency of $\mathbf{G}$ and $\boldsymbol{r}$ on the stand state $\boldsymbol{y}_t$, the model [1] is nonlinear. The matrix $\mathbf{G}$ and vector $\boldsymbol{r}$ are defined as

Fig. 2. Tree distribution on the two initial stand states used for the long-term simulations.



$$[2] \qquad \mathbf{G} = \begin{bmatrix} \mathbf{G}_1 & & & \\ & \mathbf{G}_2 & & \\ & & \ddots & \\ & & & \mathbf{G}_m \end{bmatrix},$$

$$\mathbf{G}_i = \begin{bmatrix} a_{i1} & & & & \\ b_{i1} & a_{i2} & & & \\ & \ddots & \ddots & & \\ & & b_{i,n-1} & a_{i,n-1} & \\ & & & b_{i,n-1} & a_{in} \end{bmatrix}$$

$$\boldsymbol{r} = \begin{bmatrix} \boldsymbol{r}_1 \\ \boldsymbol{r}_2 \\ \vdots \\ \boldsymbol{r}_m \end{bmatrix}, \qquad \boldsymbol{r}_i = \begin{bmatrix} R_i \\ 0 \\ \vdots \\ 0 \end{bmatrix}$$

where a_{ij} is the probability that a tree of species i and diameter class j stays alive and in the same diameter class between t and t+1, m and n are the number of species and diameter classes, respectively, b_{ij} is the probability that a tree of species i and diameter class j stays alive and grows into diameter class j+1, and R_i is the number of trees of species group i recruited in the smallest diameter class between t and t+1, with a time period of 1 year. Recruitment is zero in the higher diameter classes.

The b_{ij} probability was calculated as the annual tree diameter growth, g_{ij}, divided by the width of the diameter class. The diameter growth is a function of tree diameter D_j (cm), stand basal area B (m^2·ha^{-1}), site productivity C (m^3·ha^{-1}·year^{-1}), tree species diversity H_s, and tree size diversity H_d, with parameters α and error μ_{ij}:

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Table 5. Estimation results of diameter growth rate equations.

	Independent variable*						
	D	D^2	B	C	H_s	H_d	Constant
Douglas-fir							
Coeff.	0.0124	–0.0001	–0.0107	0.0267	0.0658	–0.2426	0.7860
SE	0.0003	0.000003	0.0002	0.0007	0.0065	0.0069	0.0118
P	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
R^2	0.34						
df	23 154						
Other shade-intolerant species							
Coeff.	–0.0038	0.0001	–0.0080	0.0170	0.0707	–0.0693	0.6104
SE	0.0006	0.000007	0.0003	0.0007	0.0096	0.0096	0.0157
P	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
R^2	0.15						
df	11 824						
Western hemlock							
Coeff.	0.0148	–0.0001	–0.0107	0.0061	–0.0250	–0.1750	0.9026
SE	0.0005	0.000004	0.0002	0.0006	0.0100	0.0092	0.0153
P	<0.0001	<0.0001	<0.0001	<0.0001	0.0128	<0.0001	<0.0001
R^2	0.40						
df	11 605						
Other shade-tolerant species							
Coeff.	0.0081	–0.00003	–0.0083	0.0178	0.1285	–0.1441	0.5851
SE	0.0004	0.000003	0.0003	0.0009	0.0136	0.0127	0.0213
P	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
R^2	0.24						
df	8893						

Note: The dependent variable, diameter growth rate, is measured in units of centimetres per year. Coeff., coefficient; SE, standard error; P, level at which the parameter would be significant; R^2, coefficient of determination; df, degrees of freedom.

*D, tree diameter (cm); B, stand basal area ($m^2 \cdot ha^{-1}$); C, site productivity ($m^3 \cdot ha^{-1} \cdot year^{-1}$); H_s, species diversity; H_d, size diversity.

[3] $$g_{ij} = \alpha_{i1} + \alpha_{i2} D_j + \alpha_{i3} D_j^2 + \alpha_{i4} B + \alpha_{i5} C + \alpha_{i6} H_s + \alpha_{i7} H_d + \mu_{ij}$$

Site productivity, measured by mean annual increment, was defined as in Hanson et al. (2002). Diversity of tree size and species are measured with Shannon's index (Magurran 1988):

[4] $$H_s = -\sum_{i=1}^{m} \frac{B_i}{B} \ln\left(\frac{B_i}{B}\right)$$

and

$$H_d = -\sum_{j=1}^{n} \frac{B_j}{B} \ln\left(\frac{B_j}{B}\right)$$

where B_i and B_j are the basal area of the trees of species group i and diameter class j, respectively.

The expected recruitment of species i is represented by a Tobit model:

[5] $$R_i = \Phi\left(\frac{\boldsymbol{\beta}_i \mathbf{x}_i}{\sigma_i}\right) \boldsymbol{\beta}_i \mathbf{x}_i + \sigma_i \phi\left(\frac{\boldsymbol{\beta}_i \mathbf{x}_i}{\sigma_i}\right)$$

with:

[6] $$\boldsymbol{\beta}_i \mathbf{x}_i = \boldsymbol{\beta}_{i1} + \boldsymbol{\beta}_{i2} B + \boldsymbol{\beta}_{i3} N_i + \boldsymbol{\beta}_{i4} C + \boldsymbol{\beta}_{i5} H_s + \boldsymbol{\beta}_{i6} H_d + \nu_i$$

where N_i the number of trees per hectare in species group i; Φ and ϕ are, respectively, the standard normal cumulative and density functions; and σ_i is the standard deviation of the residuals ν_i obtained in the estimation of the parameters β.

The probability of tree mortality per year, $m_{ij,}$ is a species-dependent probit function of tree size and stand state:

[7] $$m_{ij} = \frac{M_{ij}}{T} = \frac{1}{T} \Phi(\delta_{i1} + \delta_{i2} D_{jt} + \delta_{i3} D_{jt}^2 + \delta_{i4} B_t + \delta_{i5} C + \delta_{i6} H_{st} + \delta_{i7} H_{dt} + \xi_{ij})$$

where M_{ij} is the probability that a tree of species i and diameter class j dies within T years, δs are parameters, and ξ_{ij} is the error. Because mortality rates are small, this linear interpolation is practically identical to an exponential interpolation.

The probability that a tree stays alive and in the same size class from t to t+1 is, then

[8] $$a_{ij} = 1 - b_{ij} - m_{ij}$$

For a stand that grows according to eq. 1, the expected stand volume at time t is

[9] $$v_i = \mathbf{v}' \mathbf{y}_t$$

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Fig. 3. Effect of each explanatory variable on the expected diameter growth. The explanatory variable varies between its smallest and largest observed value while other variables are held constant at their sample means.

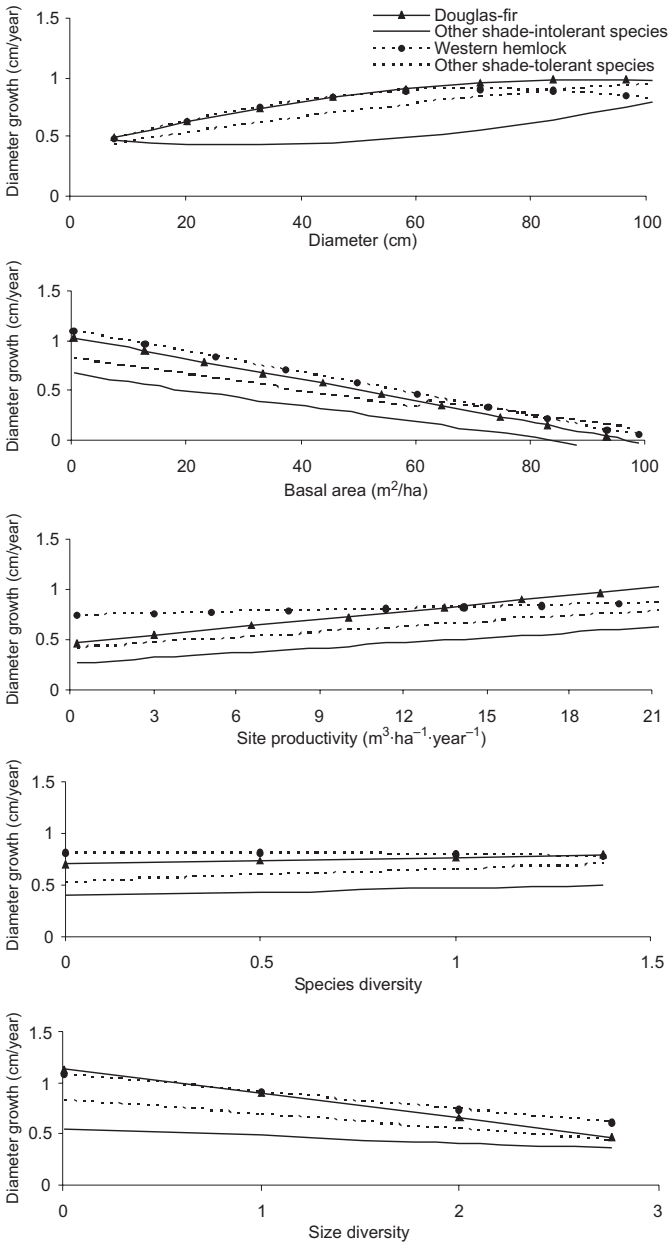
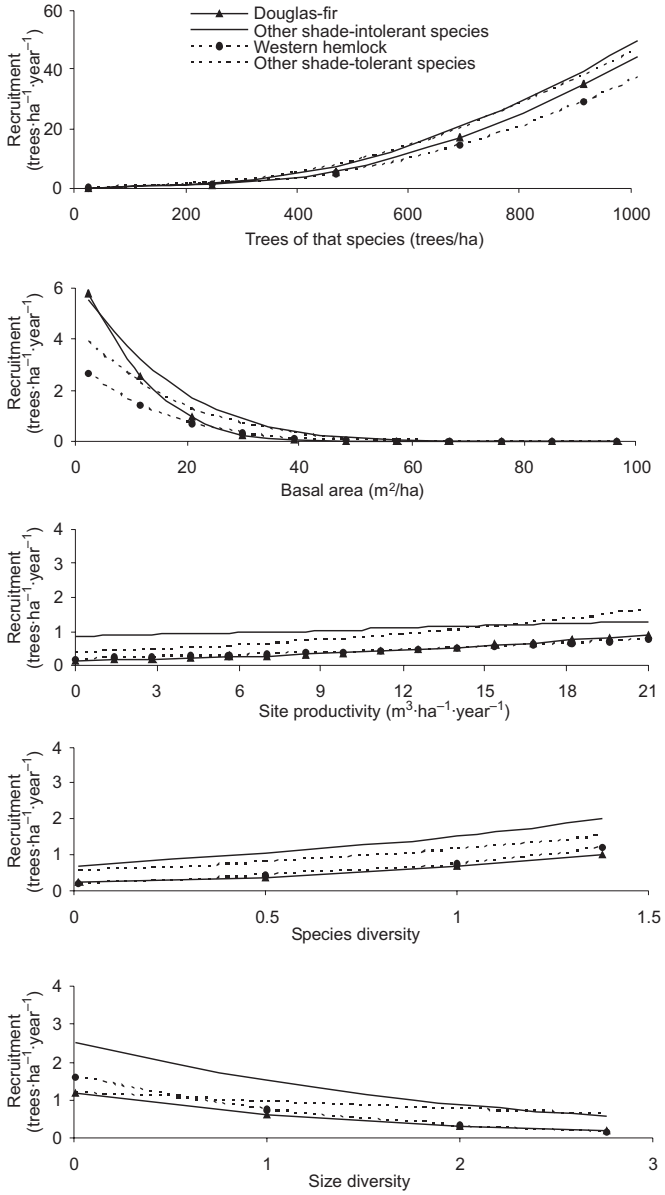


Fig. 4. Effect of each explanatory variable on the expected tree recruitment. The explanatory variable varies between its smallest and largest observed value while other variables are held constant at their sample means.



where $\mathbf{v}' = [v_{ij}]$ is a row vector and v_{ij} is the volume of a tree of species group i and diameter class j. v_{ij} is a species-dependent function of tree and stand characteristics:

$$[10] \quad v_{ij} = \lambda_{i1} + \lambda_{i2}D_j + \lambda_{i3}D_j^2 + \lambda_{i4}B + \lambda_{i5}C + \lambda_{i6}H_s + \lambda_{i7}H_d + \omega_{ij}$$

where the λs are parameters and ω_{ij} is the error.

Data

The data to estimate the parameters of eqs. 3, 6, 7, and 10 came from the Pacific Northwest - Forest Inventory and Analysis (PNW-FIA) Integrated Database (version 1.2) (Hiserote and Waddell 2003). The part of the database used here combines information from four different forest inventories (FIAEO, FIAWO, FIAEW, FIAWW) conducted by the USDA Forest Service between 1988 and 2000.

The 2706 plots selected for this study met the following criteria: all had been classified in the Douglas-fir – western hemlock forest type, they had been measured at two successive inventories, and they were located in Oregon and Washington west of 120°W (Fig. 1). Generally speaking, this area includes the Coast Range and the Cascades Range of western Washington and Oregon, as well as the Klamath region of southwestern Oregon. About 80% of the plots were on private land, and most of the remaining 20% were on lands belonging to the states of Oregon or Washington (Table 2). Note that US federal lands (e.g., national forests, national

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Table 6. Estimation results of Tobit recruitment equations.

	Independent variable*						
	N	*B*	*C*	H_s	H_d	Constant	σ
Douglas-fir							
Coeff.	0.0971	–1.2996	0.8007	11.1191	–6.8020	–21.9317	23.5471
SE	0.0025	0.0962	0.1697	2.2397	1.7545	2.7677	0.7511
P	<0.0001	<0.0001	<0.0001	<0.0001	0.0001	<0.0001	
L	–2726.12						
n	510, 2706						
Other shade-intolerant species							
Coeff.	0.0975	–0.8293	0.2032	8.4122	–5.9733	–23.6333	22.4354
SE	0.0026	0.0916	0.1604	2.2909	1.7272	2.5264	0.6120
P	<0.0001	<0.0001	0.2054	0.0002	0.0005	<0.0001	
L	–2264.27						
n	399, 2706						
Western hemlock							
Coeff.	0.0926	–0.9359	0.6699	14.6929	–9.8919	–30.8842	27.3244
SE	0.0033	0.1061	0.1907	3.1083	2.4889	3.3768	0.9340
P	<0.0001	<0.0001	0.0004	<0.0001	<0.0001	<0.0001	
L	–1912.44						
n	319, 2706						
Other shade-tolerant species							
Coeff.	0.0924	–0.7512	0.7375	8.0361	–2.2701	–34.5350	23.0297
SE	0.0034	0.0914	0.1801	2.6779	1.9950	3.3919	1.0459
P	<0.0001	<0.0001	<0.0001	0.0027	0.2552	<0.0001	
L	–1614.10						
n	278, 2706						

Note: The dependent variable, recruitment, is measured in units of trees per hectare per year. Coeff., coefficient; SE, standard error; *P*, level at which the parameter would be significant; R^2, coefficient of determination; *L*, log-likelihood value; *n*, number of plots with recruitment, total number of plots; σ, standard deviation of residuals.

*N, number of trees of that species (trees·ha^{-1}); B, stand basal area (m^2·ha^{-1}); C, site productivity (m^3·ha^{-1}·year^{-1}); H_s, species diversity; H_d, size diversity.

parks, and Bureau of Land Management forests) are not included in this database.

The trees were categorized into four species classes (Table 1): Douglas-fir, other shade-intolerant species, western hemlock, and other shade-tolerant species (Barbour and Billings 1988). Red alder and *Pinus ponderosa* Dougl. ex P. & C. Laws. (ponderosa pine) were the most abundant shade-intolerant species other than Douglas-fir. Western redcedar and bigleaf maple were the most abundant shade-tolerant species other than western hemlock (Table 1). Within each species, trees were grouped into nineteen 5.08-cm (2-in.) diameter classes, from 7.6 to 12.7 cm up to 99.1 cm and above. The average number of trees per hectare over all the plots decreased exponentially with tree diameter.

The plot characteristics are summarized in Table 3. The theoretical maximum species diversity is ln(4) = 1.39, and the maximum size diversity is ln(19) = 2.94, occurring when all the basal area is equally distributed in all 4 species classes and 19 size classes, respectively. There was a 0.90 correlation between the diversity by species group, used here, and the diversity by individual species. The average recruitment was highest for Douglas-fir and other shade-intolerant trees (Table 3).

The individual tree data (Table 4) show that, on average, Douglas-fir trees had the highest diameter growth rate and the lowest mortality rate. Other shade-tolerant species had the highest single-tree gross volume. Although the time between measurements was short, averaging a decade, there was much difference in trees and stand conditions between plots. It is this cross-sectional variation that allows an inference on how stands would grow in very different conditions that might arise in space and over long time periods.

Parameter estimation

The parameters of the diameter growth eq. 3, mortality eq. 7, and tree volume eq. 10 were estimated with individual tree data (Table 4), together with data from the plot in which each tree was growing. The Tobit recruitment equation (eq. 5) was estimated with plot data only (Table 3), by maximum likelihood. The diameter growth and tree volume equations were estimated by ordinary least squares. The probit equation of mortality, M_{ij}, was estimated by maximum likelihood, with the dependent variable equal to one if a tree died between two inventories and zero otherwise. T was the average time between the two inventories, equal to 10.53 years.

The form of the equations and the variables that they contained was decided according to their agreement with the expected biological response, their statistical characteristics (Draper and Smith 1998), and their parsimony in terms of number of parameters and function form. Though rarely used in biometrics, the Tobit form of the recruitment model was

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Table 7. Estimation results of probit mortality equations.

	Independent variable*						
	D	D^2	B	C	H_s	H_d	Constant
Douglas-fir							
Coeff.	–0.0356	0.0002	0.0081	–0.0200	0.0059	0.5110	–2.1103
SE	0.0021	0.0000	0.0014	0.0048	0.0492	0.0537	0.0933
P	<0.0001	<0.0001	<0.0001	<0.0001	0.9045	<0.0001	<0.0001
L	–2831.66						
n	677, 23 838						
Other shade-intolerant species							
Coeff.	–0.0204	0.0002	0.0053	–0.0147	0.0022	0.1411	–1.4063
SE	0.0029	0.0000	0.0017	0.0039	0.0546	0.0535	0.0823
P	<0.0001	<0.0001	0.0021	0.0001	0.9678	0.0083	<0.0001
L	–2986.44						
n	819, 12 650						
Western hemlock							
Coeff.	–0.0416	0.0003	0.0156	0.0230	0.3252	0.4192	–3.1746
SE	0.0032	0.0000	0.0018	0.0050	0.0858	0.0816	0.1615
P	<0.0001	<0.0001	<0.0001	<0.0001	0.0001	<0.0001	<0.0001
L	–1576.21						
n	395, 12 007						
Other shade-tolerant species							
Coeff.	–0.0093	–0.0000	–0.0042	–0.0303	–0.2721	0.3528	–1.5188
SE	0.0022	0.0000	0.0018	0.0053	0.0773	0.0734	0.1264
P	<0.0001	0.0535	0.0190	<0.0001	0.0004	<0.0001	<0.0001
L	–1579.20						
n	395, 9295						

Note: The dependent variable, mortality, equals one if a tree died between the two inventories, otherwise it equals zero. Coeff., coefficient; SE, standard error; P, level at which the parameter would be significant; R^2, coefficient of determination; L, log-likelihood value; n, number of plots with recruitment, total number of plots.

*D, tree diameter (cm); B, stand basal area ($m^2 \cdot ha^{-1}$); C, site productivity ($m^3 \cdot ha^{-1} \cdot year^{-1}$); H_s, species diversity; H_d, size diversity.

deemed essential because many plots had zero recruitment. The probit mortality model was consistent with the binary form of the data. Although more complex forms of the models were also tested, linear terms were sufficient for all the variables, except for the square of tree diameter, in agreement with previous results (Buongiorno et al. 1995; Ralston et al. 2003). The highest correlation among the dependent variables was 0.38 (between site productivity and basal area), and the highest variance inflation factor was merely 3.2 for other shade-tolerant species; therefore there was no evidence of multicollinearity (Belsley et al. 1980).

After an equation was estimated, the sensitivity of the dependent variables (diameter growth, recruitment, mortality, and tree volume) to a change in one independent variable was examined by varying one independent variable over the range observed in the sample while holding the other variables constant at their sample mean. Based on previous studies (Buongiorno et al. 1995; Lin et al. 1998; Ralston et al. 2003; Schulte and Buongiorno 2004), we expected that the diameter growth would be positively correlated with tree size and site productivity and negatively correlated with stand basal area. Recruitment of a species would have a positive correlation with site productivity and the density of trees of the same species, but a negative correlation with stand basal area. Mortality would decrease with tree size, but increase with stand basal area. Regarding the effects of diversity on productivity, insignificant negative relationships (Chen and Klinka 2003) are as common as positive ones (Caspersen and Pacala 2001).

Prediction errors

The accuracy of the complete model was determined by the prediction errors, the differences between the actual number of trees by size and species category at the second inventory and the predicted number, conditional on the state of the plots at the first inventory. The test was done on a set of 37 postsample plots from the PNW-FIA Integrated Database (version 1.2). All the plots were located in Pend Oreille County and Spokane County, in northeastern Washington, next to northern Idaho. These plots were selected because the North Idaho variant of FVS has a recruitment module for many of the same species, allowing a comparison of the FVS model with the present model. The plots had not been used in calibrating the model presented in this paper. They were all of the Douglas-fir – western hemlock type, with average site index 34 m. The average time interval between successive measurements on the postsample plots was 11 years. The present model was also tested on 118 plots in Northern California, of the same forest type, with results similar to those obtained with the plots in northeastern Washington.

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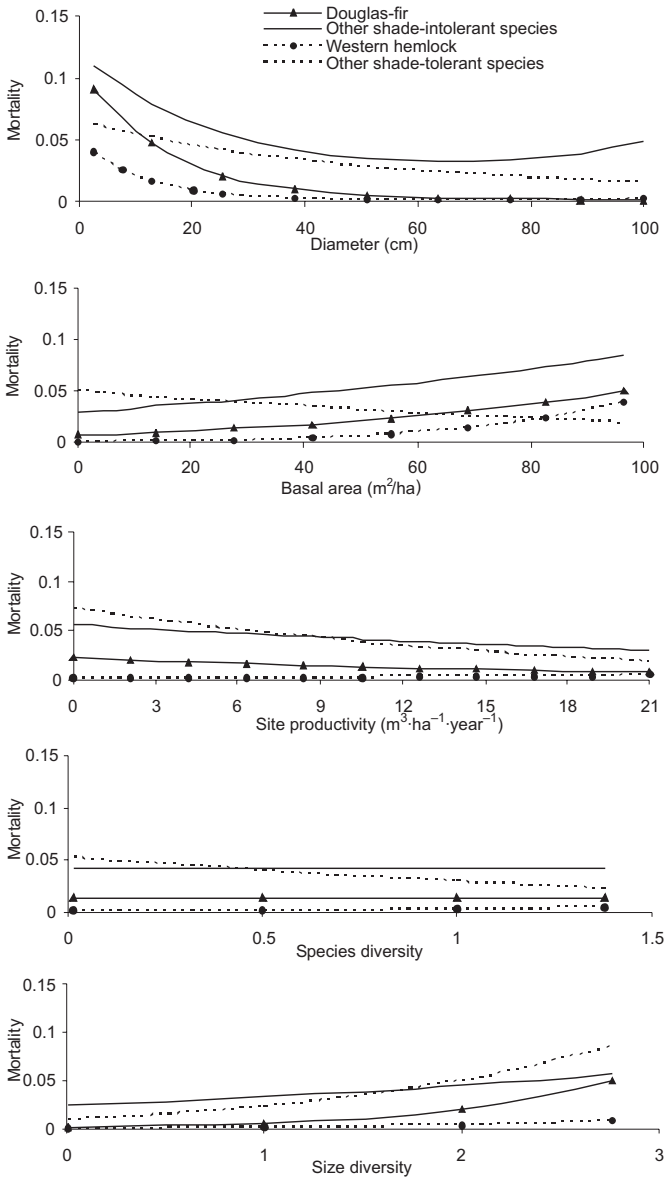
Fig. 5. Effect of each explanatory variable on mortality (probability that a tree dies between inventories spaced at an average of 10.63 years). The explanatory variable varies between its smallest and largest observed value while other variables are held constant at their sample mean.



For each plot, p, the expected number of trees at the second inventory was predicted by:

$$[11] \quad \hat{\boldsymbol{y}}_{p,0} = \boldsymbol{y}_{p,0}$$
$$\hat{\boldsymbol{y}}_{p,t+1} = \mathbf{G}\hat{\boldsymbol{y}}_{p,t} + \boldsymbol{r} \qquad t = 0,...,T_p$$

where $\boldsymbol{y}_{p,0}$ is the plot state at the first inventory and T_p is the number of years between inventories for that plot. The mean predicted number of trees by species group and diameter class over all plots, $\bar{\hat{\boldsymbol{y}}}_{ijT_p}$, was then compared with the mean observed number of trees, $\bar{\boldsymbol{y}}_{ijT_p}$.

Long-term simulations and steady state

The long-term simulations were meant to check whether the model predictions were plausible over periods much longer than the interinventory interval, for different initial states. To facilitate comparison, we chose two plots with the same site productivity, 7 $m^3 \cdot ha^{-1} \cdot year^{-1}$, which is medium-low in productivity among all the plots considered.

One simulation started with an uneven-aged multispecies stand, represented by FIA plot number 24753, located in Spokane County, northeastern Washington. Most trees were less than 50 cm in diameter, but many other species and sizes were present (Fig. 2). The initial stand basal area was 39 $m^2 \cdot ha^{-1}$, and the initial stem density was 1282 trees$\cdot ha^{-1}$.

The other simulation started with an even-aged Douglas-fir stand, represented by FIA plot number 27927, located in Skamania County, southwestern Washington (Fig. 2). The initial stand basal area was 60 $m^2 \cdot ha^{-1}$, and the initial stem density was 875 trees$\cdot ha^{-1}$. The stand was 90 years old and overstocked according to the yield tables (McArdle et al. 1961).

The long-run properties of the model were also investigated by checking whether the model had a steady state, that is to say, a stand state $\boldsymbol{y}^*$ that solved the set of nonlinear equations:

$$[12] \quad \boldsymbol{y}^* = \mathbf{G}\boldsymbol{y}^* + \boldsymbol{r}$$

More confidence could be placed in the model if this steady state existed, was unique and independent of the initial conditions, and plausible compared to the expected climax state of the forests of interest.

Results

Estimates of parameters

The estimates of the parameters in the diameter growth equations (Table 5) and the attendant sensitivity analysis in Fig. 3 show that the trees grew faster when they were larger, and the diameter growth declined with stand basal area, for all species. Trees grew faster on the better sites, regardless of species. This effect was strongest for Douglas-fir and weakest for western hemlock (Fig. 3). Diameter growth of all species decreased significantly with higher tree size diversity, and it increased slightly with species diversity, except for western hemlock. The coefficients of determination of the equations are less than 50%. This is typical of models that use the diameter growth rate as the dependent variable. It does not mean that the models are bad, but rather that the growth rate is nearly a constant plus a random term. Nevertheless, the variables used here did influence the growth rate systematically and as expected and were therefore retained. A better test of the quality of the growth equations is the postsample performance of the complete model of which they are a part, as described further.

The maximum likelihood estimates of the parameters of the recruitment eq. 5 are summarized in Table 6, and the effect of each variable is charted in Fig. 4. The recruitment of a species increased strongly with the density of that species in the stand. The rate of increase was slowest for western hemlock. For all the species, recruitment declined as the stand basal area increased. At low basal area, recruitment was 50%–100% higher for Douglas-fir and other shade-intolerant species than for western hemlock and other shade-tolerant species. There was more recruitment on more productive sites. The recruitment for all the species was positively cor-

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Table 8. Estimation results of tree volume equations.

	Independent variable*						
	D	D^2	B	C	H_s	H_d	Constant
Douglas-fir							
Coeff.	–0.0119	0.0012	0.0132	0.0293	–0.1249	–0.0330	–0.6116
SE	0.0010	0.0000	0.0000	0.0010	0.0110	0.0110	0.0200
P	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0024	<0.0001
R^2	0.96						
df	23 154						
Other shade-intolerant species							
Coeff.	0.0038	0.0009	0.0044	0.0173	0.0136	0.0358	–0.5487
SE	0.0009	0.000009	0.0005	0.0010	0.0141	0.0135	0.0233
P	<0.0001	<0.0001	<0.0001	<0.0001	0.3339	0.0083	<0.0001
R^2	0.89						
df	11 824						
Western hemlock							
Coeff.	–0.0141	0.0013	0.0072	0.0104	–0.0659	0.0516	–0.4621
SE	0.0010	0.0000	0.0000	0.0010	0.0160	0.0140	0.0260
P	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.0003	<0.0001
R^2	0.96						
df	11 605						
Other shade-tolerant species							
Coeff.	–0.0170	0.0011	0.0087	0.0146	–0.2471	0.0125	–0.1401
SE	0.0020	0.0000	0.0010	0.0040	0.0600	0.0540	0.0930
P	<0.0001	<0.0001	<0.0001	0.0001	<0.0001	0.8167	0.1323
R^2	0.85						
df	8893						

Note: The dependent variable, tree volume, is measured in units of cubic metres. Coeff., coefficient; SE, standard error; P, level at which the parameter would be significant; R^2, coefficient of determination; df, degrees of freedom.

*D, tree diameter (cm); B, stand basal area ($m^2 \cdot ha^{-1}$); C, site productivity ($m^3 \cdot ha^{-1} \cdot year^{-1}$); H_s, species diversity; H_d, size diversity.

related with species diversity and negatively correlated with size diversity. The effect of size diversity on recruitment was strongest for shade-intolerant species and weakest for shade-tolerant species.

No significant relationship was found between the interinventory time and mortality, presumably because there was too little variation in interinventory time. The mean interinventory time used in eq. 7 was $T = 10.53$ years (Table 3). The results of estimation of the mortality equations (Table 7) and the attendant Fig. 5 show that the probability of dying declined monotonically with tree diameter for most species. This is consistent with previous results (Lin et al. 1998; Schulte and Buongiorno 2004; Zenner 2005). Only for other shade-intolerant species did mortality increase slightly for the largest trees. For most species, except for the other shade-intolerant species, mortality increased significantly with stand basal area. Mortality was lower on more productive sites for all species, except for western hemlock. Other things being equal, western hemlock had the lowest mortality. There was practically no relation between mortality and species diversity, but mortality increased with tree size diversity, especially for Douglas-fir.

According to the parameters of the tree volume equations (Table 8), tree volume was most strongly related to tree diameter. The relation between gross volume and stand basal area was positive but weak. Although statistically significant, the positive relation between tree volume and site productivity was also weak. There was practically no relationship between individual tree volume and species and size diversity.

Prediction errors

Figure 6 shows the errors in predicting the number of trees on the 37 postsample plots in northeastern Washington at the second inventory, conditional on the number at the first inventory. The predictions of this model all fell within the 95% confidence interval of the observations. For Douglas-fir, western hemlock, and other shade-tolerant species, there was no systematic under- or over-estimation. For other shade-intolerant species, the model slightly overestimated the number of trees that were 10–40 cm in diameter.

In comparison, the FVS significantly underestimated the number of Douglas-fir trees up to a diameter of 52 cm. For the smallest diameter classes this was partly because the FVS generates new recruitment only every 20 years, while the average interval between the inventories on the test plots was 11 years. For the larger size classes, the underestimation may be due to underestimation of tree growth or overestimation of tree mortality.

Comparisons with the WestPro model are more difficult than with the FVS because WestPro groups species according to softwoods and hardwoods only. Applied to the plots used in this study, and one interinventory period, WestPro

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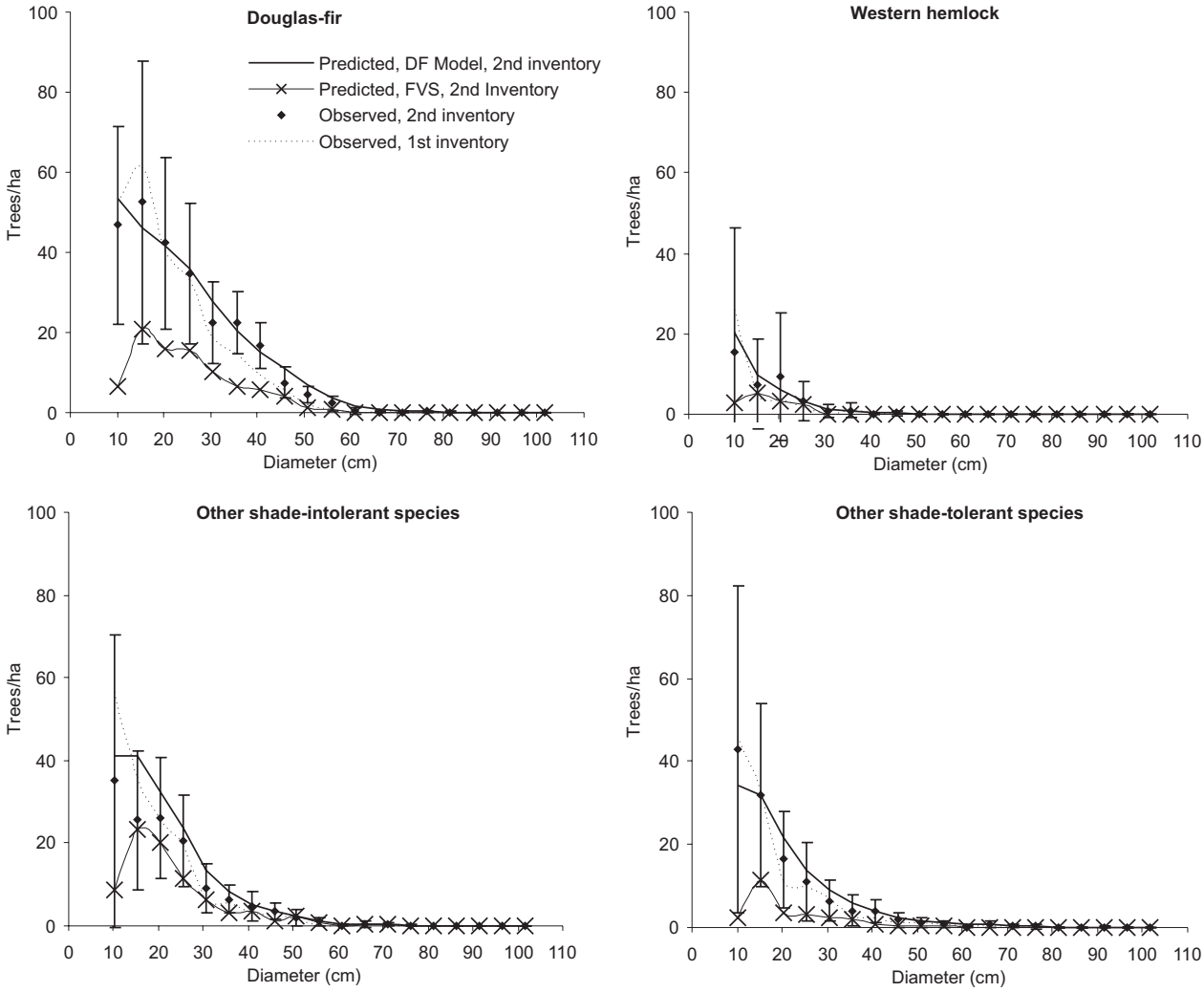
Fig. 6. Average predicted and observed (with 95% confidence interval) number of trees at the second inventory, conditional on the first inventory data set, on 37 postsample plots in Pend Oreille County and Spokane County, Washington, next to northern Idaho. Predictions were obtained with the Forest Vegetation Simulator and with the model presented here (DF).



tended to underestimate the number of softwood trees in the small diameter classes and overestimate the number of hardwood trees.

Long-term simulations

The present model predicted that for an uneven-aged multispecies stand with the initial state in Fig. 2, the number of trees would gradually decrease over 100 years, in parallel with the number predicted by the FVS (Fig. 7). The predicted total stand gross volume reached about 900 $m^3 \cdot ha^{-1}$ after 100 years, 30% more than that predicted by the FVS. The FVS predicted substantially less volume growth in the early years, presumably because it generates recruitment only every 20 years. For both models, the species diversity remained high and essentially constant over 100 years.

For the even-aged Douglas-fir stand with initial state in Fig. 2, the number of trees declined smoothly at about the same rate for the two models and for the yield tables (Fig. 7). The present model predicted that the gross volume of this initially overstocked stand would increase only slightly. The FVS also predicted a constant volume, but at a substantially lower level. Both models predicted that the stand would remain an almost pure Douglas-fir stand, so that species diversity would remain very low and about constant for 100 years.

Regardless of the initial condition, the present model predicted that the stand would eventually reach a steady state, the solution of eq. 12. We verified by simulation that the same steady state was reached with the two initial conditions in Fig. 2. In the steady state, the stand was dominated by western hemlock over 100 cm in diameter, with few trees of other species and size. Thus the steady-state diversity was quite low: 0.21 for species and 0.05 for size. The steady-state stand basal area was 70 $m^2 \cdot ha^{-1}$, and the stand volume was 1051 $m^3 \cdot ha^{-1}$.

Over 100 years, WestPro predicted systematically more trees and more volume than those predicted by the present model, the FVS, or the yield tables (Fig. 7). WestPro has a steady state independent of the initial condition. For intermediate sites, the steady state is similar in total volume to that predicted by the present model, but it consists of about 25% hardwoods (Ralston et al. 1993), while the present model predicted a steady state with almost western hemlock only. Because WestPro has only two species groups, softwoods and hardwoods, while our model and FVS have four, the

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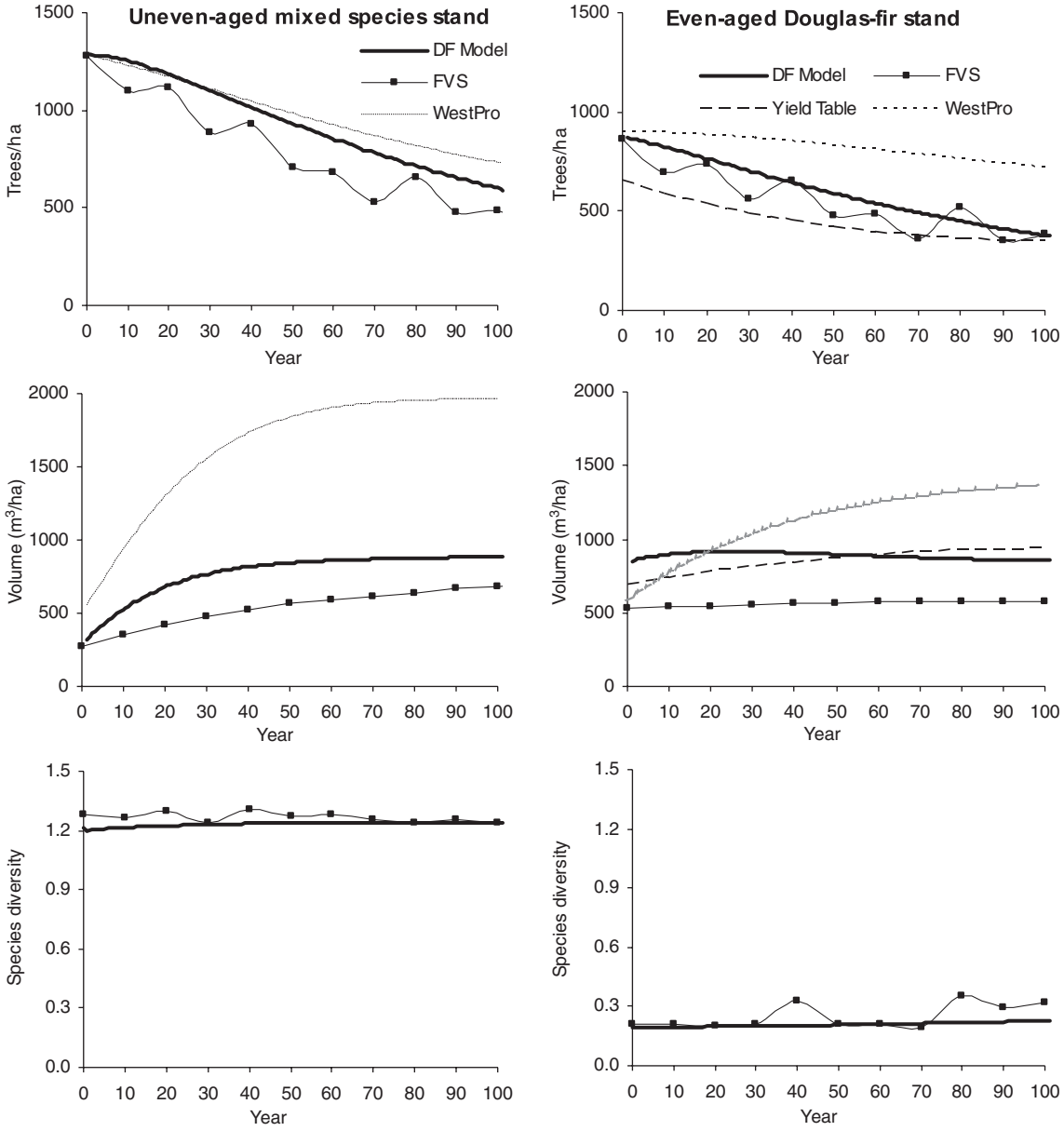
Fig. 7. Predicted growth of the two stands with the initial states described in Fig. 2. DF indicates the model presented in this paper. Yield table predictions are from McArdle et al. (1961).



comparison of species diversity from WestPro was not possible.

Discussion and conclusion

The diameter growth, recruitment, and mortality equations that underlie the model are consistent with prior expectations regarding the effects of tree diameter, stand basal area, and site productivity. There is little prior knowledge regarding the effects of stand diversity on forest growth. We found that the diameter growth increases slightly with species diversity and declines with size diversity, when other tree and stand characteristics are held constant. The recruitment is positively correlated with species diversity and negatively with size diversity. Mortality is independent of species diversity, but is positively correlated with size diversity. There is practically no relationship between individual-tree volume and the diversity of the stand in species or size. Piazza (1999) also finds a negative correlation between recruitment and tree size diversity, but no correlation between mortality and stand diversity in northern hardwood stands.

Applied on many plots and for predictions of 10–20 years, the model yields generally unbiased predictions of the number of trees of all species by diameter class. The simulation of the even-aged Douglas-fir stand predicts a number of trees and volume after 100 years similar to those of the yield tables of McArdle et al. (1961).

The longer model predictions are subject to large errors. Nevertheless, the results of the long-term simulations and the steady-state analysis are plausible given prior knowledge of the climax forests of this ecotype and the corresponding magnitude of volumes, basal area, and species composition. In particular, the predicted eventual replacement of the seral Douglas-fir by western hemlock and other shade-tolerant spe-

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cies in the absence of disturbances is in agreement with previous observations (e.g., Munger 1940; Franklin et al. 1981; Hermann and Lavender 1990).

One limitation of the present model, if it is used for long-term projections, is that the data did not distinguish plots that had been regenerated artificially. Still, the diversity variable may serve as a proxy, albeit imperfect, for the effect of artificial regeneration, because artificially regenerated stands are more likely to be even aged and monospecific and therefore less diverse in species and size.

Nevertheless, the model predictions over a few years and several decades were more accurate than those of the FVS or WestPro. Another positive feature of the present model is its stable long-term behavior. Predictions over one century, and in the steady state, meet biological expectations on stand development. Also, the model is based on a large and representative data set of the Douglas-fir – western hemlock forest type. It covers a wide range of stand structures, from even-aged monospecific stands to uneven-aged mixed species stands. Another major advantage of the model is its simple formulation and ease of use, which makes it suitable for many management applications.

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